Role of endophytic fungi in grass litter decomposition

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Abstract

Fungal endophytes of grasses affect ecosystem processes through mutualistic interactions with host plants, but how grass endophytes affect litter decomposition remains unclear. In this study, previously published data on litter quality and decomposition of grasses are summarised and effects of fungal endophytes of grasses on litter quality and decomposition are reviewed to discuss possible roles of endophytes in decomposition. Aboveground litters of grasses have relatively low nitrogen (N) and lignin contents and show slow increase of N and lignin contents during decomposition. Endophyte-infected litter have slightly lower N contents than non-infected litter, but the differences so far reported were not statistically significant. A negative effect of grass endophytes on litter decomposition rates was demonstrated, but the effect of endophyte infection on decomposition was not as strong as the effects of other biological and environmental factors. This suggests that grass endophytes have a relatively minor effect of on litter quality and decomposition, but more studies are necessary to verify this tentative conclusion.
Keywords: decomposition, lignin, litter, nitrogen

Introduction

Fungal endophytes of grasses affect ecosystem processes through mutualistic interactions with host plants. Impacts of grass endophytes on the diversity and productivity of grass and herbivore communities have been well documented, whereas their impacts on grass litter decomposition have been demonstrated only recently (Rudgers & Clay 2005). Fungal endophytes can alter decomposition directly or indirectly (Boddy & Griffith 1989; Osono 2006), but it is unclear how grass endophytes affect decomposition processes of litter. The purposes of the present study are (i) to summarise previously published data on litter quality and decomposition of grasses to define decomposition as an ecosystem process, (ii) to review and quantify the effects of grass endophytes on litter quality and decomposition, and (iii) to discuss the possible roles of endophytes in decomposition. References are made to data on litter quality and decomposition of tree leaves (Berg & McClaugherty 2003) and to the roles of foliar endophytes of trees in decomposition (Osono 2006) for comparison.

Brief Summary of Grass Litter Quality and Decomposition

Litter decomposition is an important aspect of ecosystem function that mediates the formation of soil organic matter, the evolution of carbon dioxide from soils, and the accumulation and mineralisation of soil nutrients. Decomposition thus has intimate relationships with not only the productivity and nutrient cycling within ecosystems but also the global carbon cycle. Factors affecting decomposition include: (i) litter quality such as contents of N and lignin; (ii) decomposer communities such as fungi and soil animals; and (iii) environmental factors such as temperature, moisture, and soil depth (Swift *et al.* 1979). Studies on the effects of litter quality have shown a positive effect of total N content and negative effect of lignin content on decomposition.

Aboveground litters of grasses, such as blades, sheaths, and straw, have nitrogen (N) content of 7.5 mg/g dry litter (n=82) and lignin content of 128 mg/g (n=65) on average. These values contrast to the values for tree leaf litters which have higher mean N contents (10-14 mg/g) and higher mean lignin contents (220-260 mg/g). Decomposition rates of grass litter studied under field conditions, expressed as a slope of the exponential function (Olson's *k*, Olson 1963), measure 1.09/year on average in temperate regions, which is comparable to those of tree leaf litter (*k*=1.06/year). The lower lignin content in grass litter which favours the rapid mineralisation of major structural components by decomposer organisms can be counteracted by the low N content which often limits the growth of the decomposers.

Slow increases in N and lignin contents characterises the decomposition process of grass litter (Fig.1). This again contrasts to tree leaf litters which in general show a relatively rapid increase in N and lignin contents with respect to the accumulated mass loss of litter during decomposition (Fig.1) (Berg & McClaugherty 2003). The slopes for these linear relationships with N and lignin contents are generally lower in grass litter than in tree leaf litter. A possible explanation for this difference is the interaction of N and lignin in decomposing litter discussed in Berg (1986). That is, the lower initial content of lignin in grass litter can account for the slower increase of N content during decomposition, as lignin content has been suggested as a primary factor controlling the amount of N immobilised into litter (Osono & Takeda 2004). The lower N content in grass litter, in turn, can account for the slower increase in lignin content (Berg & McClaugherty 2003).

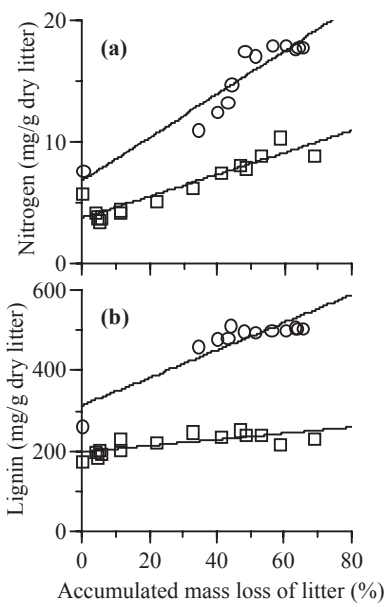

Figure 1 Changes in nitrogen (a) and lignin (b) contents during decomposition of barley (*Hordeum vulgare* L.) straw (open boxes) and birch (*Betula pubescens* Ehrh.) leaves (open circles) in Sweden. Reproduced from the original data of Berg and Wessén (1984), Wessén and Berg (1986), and Berg and Staaf (1987).

Effect of Endophytes on Litter Quality and Decomposition

A few studies have indicated that endophyte-infected litter had slightly lower N contents than non-infected litter, but the differences so far reported were not statistically significant. Omacini *et al.* (2004) found no significant difference in total N content between endophyte infected (E+) and non-infected (E-) *Lolium* litters (4.1-4.9 vs 5.1-5.5 mg/g). Lemons *et al.* (2005) also reported no significant difference in total N content between E+ and E- litters (10.4 vs 11.2 mg/g). In contrast, Lyons *et al.* (1990) reported an increase of total soluble amino acids and NH_4^+ in live *Festuca* leaves from infected plants, but this was apparent only when N fertiliser was applied at a high rate. Malinowski *et al.* (2000) also reported an increase of some minerals such as P, Ca, and Zn in live roots of infected *Festuca*. In the latter two studies, however, it is unknown whether the difference in live tissue quality between infected and non-infected plants can be reflected in litter quality.

Recent studies have demonstrated a negative effect of *Neotyphodium* endophyte on litter decomposition. Omacini *et al.* (2004) found decomposition rates to be 18% slower on average in E+ litter (k=1.28/year) than in litter not infected by endophytes (k=1.57/year) both in a garden microcosm experiment and in a greenhouse experiment. Lemons *et al.* (2005) also found decomposition rates were 6% slower in E+ litter (k=1.08/year) than in E- litter (k=1.19/year) in an agricultural field experiment. In another greenhouse pot experiment, however, the authors found decomposition rates were 5% slower in E+ than in E- litter but the difference was not statistically significant. The greater accumulation of soil carbon in high-endophyte-infected *Festuca* pastures than in low-infected ones (Franzluebbers *et al.* 1999; Schomberg *et al.* 2000) is possibly attributable to a reduction in decomposition rates of E+ litter.

The impacts of endophyte infection on litter decomposition rate are compared with the impacts of other biological and environmental factors in Table 1. Here, I arbitrarily selected mesh size as a measure of the effect of soil fauna exclusion on decomposition, and soil depth as a measure of the effect of the micro-environment at which the decomposition takes place. For the comparison, the effects are presented quantitatively in Table 1 as a percentage based on the decomposition rate of "treatment" with respect to that of "control". These data suggest a stronger effect of soil fauna-exclusion and soil depth on decomposition rates than of endophyte infection.

Discussion

Role of endophytes in modification of litter quality and micro-environment

Omacini *et al.* (2004) and Lemons *et al.* (2005) suggested that litter deposited by endophyte-infected grasses may have chemical or physical properties that reduced their suitability as a substrate for decomposers, which was probably associated with the production of toxic alkaloids. Such a negative effect of endophytes on decomposition through the production of alkaloids is likely but yet to be demonstrated. Studies are necessary on alkaloid contents in decomposing infected litter. Patterns of changes in N and lignin contents should be investigated in infected and non-infected litters to evaluate the effect of alkaloids on long-term decomposition processes. In addition, bioassays of the toxicity of alkaloids to decomposer fungi and animals can provide insights into the mechanisms underlying the effects of alkaloids on decomposition.

Further indirect effects on decomposition in micro-environments modified by grass endophytes have been demonstrated, such as the possible effects of richness and biomass of plant species and surface litter accumulation within plant communities (Omacini *et al.* 2004; Lemons *et al.* 2005). The causal relationships between decomposition and these factors are not fully resolved and should be examined in future studies.

Grass endophytes as possible decomposers

Grass endophytes have been regarded as mutualistic symbionts with their host plants; consequently, little attention has been paid to the possible roles of grass endophytes as decomposers and their direct impacts on litter decomposition. It is generally considered that grass endophytes are vertically transmitted through seeds or reproduce on live host tissues, and thus have no need to utilise dead tissues to complete their life cycle. Recently-

Table 1 A summary of changes in decomposition rate (Olson's k) of grass litter in relation to endophyte infection, mesh size, and soil depth. Values indicate min-max ranges.

Treatment	% change in decomposition rate	Number of case studies
Endophyte effect[a]		
Endophyte infection	82-95	3
Mesh size effect[b]		
Macrofauna exclusion	41-86	7
Macro- and mesofauna exclusion	36-68	4
Soil depth effect[c]		
Aerial position	12-74	6
Soil depth up to 5 cm	89-122	3
Soil depth deeper than 5 cm	59-192	7

[a] Ratio of the decomposition rate of endophyte-infected litter with respect to that of endophyte-free litter.
[b] Ratio of the decomposition rate of litter enclosed in litterbags with 1 mm mesh (macrofauna excluded) and 0.1 mm mesh (macro- and mesofauna excluded) with respect to that enclosed in litterbags with mesh sizes more than or equal to 2 mm (no exclusion).
[c] Ratio of the decomposition rate at aerial position, soil depth between 0-5 cm, and soil depth deeper than 5 cm with respect to that on the soil surface.

dead tissues, however, contain abundant soluble components; and grass endophytes are able to utilise simple sugars, such as glucose, sucrose, and xylose, as a sole carbon source (White *et al.* 1991). Endophytes thus have an advantage in being able to utilise these readily available components prior to fungi that colonise after tissue death (Osono 2006). Such an ecological advantage implies the colonisation of dead tissues by endophytes.

For foliar endophytes of forest trees, approximately two-thirds of endophytic fungal species colonise leaf litter after leaf death and directly take part in the decomposition, which in most cases results in a relative increase in lignin content in decomposing litter (e.g. Fig. 1) (Osono 2006). In contrast, there are few data on the occurrence of grass endophytes in litter and their roles in organic-chemical changes during decomposition. Further studies are needed to test potential abilities of grass endophytes to utilise organic chemical components in grass litter.

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